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Aquatic turning performance of painted turtles (*Chrysemys picta*) and functional consequences of a rigid body design

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Summary

The ability to capture prey and avoid predation in aquatic habitats depends strongly on the ability to perform unsteady maneuvers (e.g. turns), which itself depends strongly on body flexibility. Two previous studies of turning performance in rigid-bodied taxa have found either high maneuverability or high agility, but not both. However, examinations of aquatic turning performance in rigid-bodied animals have had limited taxonomic scope and, as such, the effects of many body shapes and designs on aquatic maneuverability and agility have yet to be examined. Turtles represent the oldest extant lineage of rigid-bodied vertebrates and the only aquatic rigid-bodied tetrapods. We evaluated the aquatic turning performance of painted turtles, *Chrysemys picta* (Schneider, 1783) using the minimum length-specific radius of the turning path (*R/L*) and the average turning rate (ω_{avg}) as measures of maneuverability and agility, respectively. We filmed turtles conducting forward and backward turns in an aquatic arena. Each type of turn was executed using a different pattern of limb movements. During forward turns, turtles consistently protracted the inboard forelimb and held it stationary into the flow, while continuing to move the outboard forelimb and both hindlimbs as in rectilinear swimming. The limb movements of backward turns were more complex than those of forward turns, but involved near simultaneous retraction and protraction of contralateral fore- and hindlimbs, respectively. Forward turns had a minimum *R/L* of 0.0018 (the second single lowest value reported from any animal) and a maximum ω_{avg} of 247.1°. Values of *R/L* for backward turns (0.0091–0.0950 *L*) were much less variable than that of forward turns (0.0018–1.0442 *L*). The maneuverability of turtles is similar to that recorded previously for rigid-bodied boxfish. However, several morphological features of turtles (e.g. shell morphology and limb position) appear to increase agility relative to the body design of boxfish.

Key words: biomechanics, locomotion, swimming, performance, maneuverability, turtle.

Introduction

Locomotor performance is important to the survival of nearly all vertebrates. Whereas the importance of some components of locomotor performance, such as rectilinear sprint speed and endurance, is widely appreciated, many other aspects of locomotion can also be critical to an animal's survival (Biewener and Gillis, 1999; Blob et al., 2006). For example, animals rarely move in a straight line for prolonged durations. Animals that live in complex habitats or engage in predator-prey interactions may need to change direction frequently as they negotiate obstacles or attempt to evade predators or capture food. Thus, turning performance may be a critical aspect of locomotion for many animals (Howland, 1974; Gerstner, 1999; Domenici, 2001; Hedenström and Rosén, 2001).

Turns generally incorporate two types of motion: (1) rotation about a vertical axis through the center of an organism (reorientation), and (2) translation of this axis (i.e. the center-of-rotation) across a horizontal plane (Howland, 1974; Norberg and Rayner, 1987; Webb, 1994). Turning performance can be measured with respect to both of these types of motion. The speed of reorientation is generally measured as agility, which can be defined as the angular velocity about a center-of-rotation on the animal (i.e. ω, the turning rate), with higher values indicating superior performance (Webb, 1994). Performance with respect to translational movement is generally termed maneuverability, which is defined as the ability to turn in a limited space (Norberg and Rayner, 1987). Maneuverability is most commonly measured as the minimum radius of the turning path [denoted as *R* (Howland, 1974)]. For *R*, performance is considered to increase as turning radii decrease. Thus, maximal turning performance is attained through superior values of both agility and maneuverability (i.e. high values of ω and low values of *R*).

Over the past few decades, several studies have investigated the effects of particular morphologies on turning performance

(Norberg and Rayner, 1987; Carrier et al., 2001; Fish, 2002; Walter and Carrier, 2002). Among aquatic animals, studies of turning performance have focused primarily on actinopterygian fishes (Webb and Keyes, 1981; Webb, 1983; Blake et al., 1995; Schrank and Webb, 1998; Gerstner, 1999; Walker, 2000; Webb and Fairchild, 2001), though a few studies have also examined turning performance in chondrichthyans (Kajiura et al., 2003; Domenici et al., 2004), cetaceans (Fish, 2002), pinnipeds (Fish et al., 2003), penguins (Hui, 1985), squid (Foyle and O'Dor, 1988) and beetles (Fish and Nicastro, 2003). For aquatic taxa, morphological attributes that are correlated with turning performance include: body shape, the position and mobility of propulsors and control surfaces (e.g. fins, flippers and limbs), and body flexibility (Blake et al., 1995; Fish, 1999; Fish, 2002; Walker, 2000; Fish and Nicastro, 2003). Body flexibility varies substantially among different aquatic animals, ranging along a continuum from animals that are highly flexible to those that are unable to bend their body axis. Along this continuum, three broad categories of body design can be recognized: flexible, stiff and rigid. Animals with flexible bodies can bend their body axis easily; examples include many ray-finned fishes, especially those inhabiting complex environments (Domenici and Blake, 1997). Animals with stiff bodies have a more limited capacity to bend the body axis and include many pelagic swimmers, such as thick-skinned tuna and many cetaceans (Blake et al., 1995; Fish, 2002). Finally, animals with rigid bodies are completely inflexible and have no capacity to bend the body axis. Rigid body designs can be found in many animals with exoskeletons, shells, or other forms of body armor (Walker, 2000; Fish and Nicastro, 2003).

Flexibility of the body is thought to enhance turning performance for several reasons (Fish, 1999; Fish, 2002; Walker, 2000). First, having a flexible body allows an organism to turn in a circular space with a radius of less than 0.5 body lengths (*L*), the theoretical minimum for a rigid structure turning with no translation (Walker, 2000). Second, flexibility of the body allows animals to reduce their second moment of area about the rotational axis, thereby decreasing rotational inertia (Walker, 2000; Walter and Carrier, 2002). Conversely, a rigid body should impair both of these advantages of body flexibility. Although turning performance has been studied in a large number of diverse flexible- and stiff-bodied species, explicit evaluations of turning performance among rigid-bodied animals have been limited to one invertebrate and one vertebrate: whirligig beetles (Fish and Nicastro, 2003) and boxfish (Walker, 2000). The results of these studies have led to differing conclusions as to whether rigid body designs actually constrain turning performance. In particular, boxfish can turn with a very small radius (i.e. are highly maneuverable), but turn fairly slowly [i.e. have low agility (Walker, 2000)]. In contrast, whirligig beetles display high angular velocities (i.e. high agility) during turns, but also have large turning radii [i.e. low maneuverability (Fish and Nicastro, 2003)].

Because examinations of aquatic turning performance in rigid-bodied animals have had a limited taxonomic scope, the effects of many body shapes and designs on aquatic maneuverability and agility have yet to be evaluated. One group of vertebrates that provides an ideal system in which to evaluate the effects of rigid bodies on aquatic turning performance is the turtles. Turtles represent the oldest extant group of rigid-bodied vertebrates and the only such group of tetrapods (Rieppel and Reisz, 1999; Santini and Tyler, 2003). The chelonian bauplan represents an evolutionary novelty that has remained relatively unchanged for over 200 million years (Burke, 1989; Gaffney, 1990). In turtles, the vertebrae are fused dorsally with a bony carapace, precluding movement of the axial skeleton between the base of the neck and the tail. As a result of their immobilized axial skeleton and reduced tail, thrust in swimming turtles is generated exclusively by the movements of fore- and hindlimbs (Pace et al., 2001). Despite the potential constraints of a rigid body on locomotion in turtles, over 100 species currently live in freshwater and marine habitats. Freshwater species in particular have adapted to life in a diverse array of aquatic flow regimes, ranging from ponds and lakes to fast flowing rivers, while also maintaining the ability to move efficiently on land (Ernst et al., 1994). Although morphological data suggest that the shells of freshwater turtles are highly suited for movement through aquatic habitats (Aresco and Dobie, 2000; Claude et al., 2003), examinations of swimming performance in freshwater turtles have been limited. Knowledge of aquatic locomotion in freshwater turtles consists mainly of studies of limb kinematics during rectilinear swimming or underwater walking (Zug, 1971; Davenport et al., 1984; Pace et al., 2001; Willey and Blob, 2004). No study has yet evaluated how turtles generate turns, or quantified any aspect of turning performance for species in this lineage. Because they possess a very different body design than that of boxfish (with a dorsoventrally flattened body shape and jointed limbs, rather than flexible fins, as propulsors) turtles provide an important comparison for evaluating the effects of morphological design on hydrodynamic performance in vertebrates.

To gain insight into the effects of body design on aquatic turning performance, we measured the performance of aquatic turns by painted turtles (*Chrysemys picta*), a freshwater species that exhibits a generalized morphology typical of the emydid turtle clade (Ernst et al., 1994). The specific objectives of this work were twofold. First, we measured limb kinematics in turning turtles in order to evaluate the mechanisms used by turtles to produce turns. Second, we compared the turning performance of painted turtles with that previously measured from other taxa in order to further evaluate the effects of different body designs on aquatic locomotor performance.

Materials and methods

Experimental animals

Turns were performed by six yearling painted turtles *Chrysemys picta* (Schneider, 1783). Carapace lengths ranged from 3.80 to 6.16 cm (mean, 4.76 cm) and masses from 10.7 to 40.4 g (mean, 21.8 g). Turtles were obtained from a commercial turtle farm (Concordia Turtle Farm, Wildsville,

LA, USA) and housed together in a large, water filled plastic tub (91 cm×61 cm×20 cm), located in a climate-controlled greenhouse at Clemson University (Clemson, SC, USA). This housing arrangement exposed turtles to ambient light patterns and temperatures during the course of the experiments, which were conducted during June and July 2005. The tank was fitted with a water filter and a dry platform for basking, and turtles were fed commercial pellets four times a week. All animal care and experimental procedures followed Clemson University IACUC guidelines (protocol 50025).

Turning data collection

Aquatic turns were elicited from turtles by stimulating predatory behavior. Each turtle was placed individually into a 75.7 l glass aquarium filled with water to a depth of 10 cm. A Plexiglas divider was used to create a 30 cm×30 cm test arena, and a submerged 100 W heater (located inside the aquarium, but outside of the test arena) maintained water temperature between 24 and 28°C. For each trial, one (or, in some cases, two) small goldfish (*Carassius auratus*) were added to the test arena as prey for the turtle. After introduction of the prey, turtles attempted to catch the fish by chasing them around the tank, often executing turns in the process. Occasionally, turtles could not be incited to chase the fish, either at the beginning of a test day or following pursuits. These trials were halted after 30 min of inactivity and turtles were returned to their holding tank to be tested again the following day.

Turns that each turtle executed as it chased fish were filmed (150 Hz) simultaneously in ventral and lateral views using two digitally synchronized high-speed video cameras (Phantom V4.1,Vision Research, Inc., Wayne, NJ, USA). The ventral view was captured using a mirror placed at 45° to the tank bottom, which allowed a camera to be focused on a central 25×25 cm area that was delineated on the transparent bottom of the test arena. As a result, turns that occurred within 2.5 cm of the sides of the arena (~0.5 *L*; body length) were not entirely within the field of view and were excluded from analysis; this allowed us to ensure that turtles conducted turns without contacting the sides of the arena. A 1 cm square grid filmed in the ventral view for each trial provided a distance calibration for video analyses (see below). Lateral view videos for each trial were reviewed to ensure that turtles were not in contact with the bottom of the tank, and that they remained level (less than ±15°) and in a horizontal plane throughout the turn. Any turn that did not conform to these criteria also was excluded from analysis. Acceptable trials were downloaded to a computer as proprietary format CINE (.cin) files and converted to AVI format for analysis.

Turning data analysis

To begin quantifying aquatic turning kinematics and performance in turtles, the positions of landmarks on their bodies were first digitized from ventral-view AVI video files using a modification of the public domain NIH Image program for Macintosh, developed at the US National Institutes of Health and available on the internet at http://rsb.info.nih.gov/nih-image/ (the modification, QuickImage, was developed by J. Walker and is available online at http://www.usm.maine.edu/~walker/software.html). Nineteen points were digitized on every other video frame, yielding effective framing rates of 75 Hz. These points were located on the head (tip of snout), plastron (six points along the midline: anterior edge, humeral–pectoral suture, pectoral–abdominal suture, abdominal–femoral suture, femoral–anal suture and posterior edge), forelimbs (shoulder, elbow and distal tip of manus) and hindlimbs (hip, knee and distal tip of pes; Fig. 1).

To evaluate the kinematic patterns that turtles used to produce aquatic turns, coordinate data were input into a custom Matlab (Ver. 7, Mathworks, Inc.; Natick, MA, USA) routine that calculated the movements of each of the four limbs throughout the course of each trial. Each limb was defined as a vector marked by the endpoints of its proximal segment (forelimb: shoulder and elbow; hindlimb: hip and knee). The position of each limb was calculated using standard equations for the angle between two vectors, with the proximal limb segment (humerus or femur) forming the first vector, and the midline axis of the body forming the second. Angles were calculated from the ventral-view videos as two-dimensional projections onto the horizontal plane. A limb segment parallel to the midline axis and oriented cranially was assigned an angle of 0°, whereas one parallel to the midline and oriented caudally was assigned an angle of 180°.

To evaluate maneuverability for each turn, the software QuicKurve (Walker, 1998a) was used to interpolate 100 equidistant points along the line of best fit through the six midline landmarks of the plastron for each digitized frame of every trial. For each turn, these coordinate data (100 midline points per frame) were input into a custom Matlab routine, which calculated the position of the turtle's center-of-rotation (COR) as it moved along the curved turning path. The COR was calculated as the point along the turtle's midline that traveled the smallest cumulative distance throughout the turn (sensu Walker, 2000) and is used to define the turning path. We

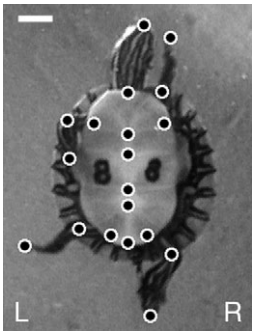


Fig. 1. Ventral view of a painted turtle with 19 digitized landmarks. The number 8, visible on the plastron, was used for identification purposes. R and L refer to the right and left sides of the turtle, respectively. Note that because the ventral view is reflected by a mirror, the left side of the animal appears on the left side of the image. Scale bar, 1 cm.

then used QuicKurve (Walker, 1998a) to fit a quintic spline to the *x*-*y* coordinates of the COR along the turning path (Woltring, 1986; Walker, 1998b), smoothing the data and allowing us to compute the local (i.e. instantaneous) curvature, κ, along the path using the parametric function:

$$\kappa = |x'y''-y'x''| / [(x')^2+(y')^2]^{3/2} ,$$

where $'$ and $''$ reflect the first and second derivative of x and y, respectively. Finally, the instantaneous radius of the curved turning path is obtained by calculating the reciprocal of κ; the smallest of these values is the minimum instantaneous radius, *R*. For each turn, *R* was used as an index of maneuverability. Length-specific turning radii (*R*/*L*) were calculated to adjust for differences in size of individual turtles, and between turtles and other taxa. In addition, the average and maximum tangential velocity of the COR (U_{avg} and U_{max}, respectively) were calculated for each trial to examine the relationship between tangential velocity (i.e. velocity along the curved turning path) and the length-specific minimum radius of the turning path, *R*/*L*. Tangential velocity (*U*, in $L\,s^{-1}$) was calculated from differentiation of the cumulative displacement of the COR along the turning path (based on the positional data). Differentiation was performed using QuickSAND software (available online at http://www.usm.maine.edu/~walker/software.html). Prior to differentiation, data were smoothed in QuickSAND using a quintic spline and the generalized cross validation smoothing option (Walker, 1998b). The largest value during a trial represented U_{max}, whereas U_{avg} represents the mean of all values during a trial.

Midline coordinate data from each turn were also input into a custom Matlab routine to calculate, (1) cumulative angular rotation of the midline from its initial orientation (i.e. at the beginning of the turn), and (2) the maximum angle of the turn. Angular rotation was calculated using standard equations for the angle between two vectors, with the vectors defined by the positions of the anterior and posterior edges of the plastron in the initial frame of the turn and in each digitized frame thereafter. Using the values obtained for cumulative angular rotation, the instantaneous angular velocity (ω) (i.e. the angular velocity between each pair of sequentially digitized frames) was calculated in QuickSAND software using the procedures described above for measures of tangential velocity (*U*). The largest value during a trial represented the maximum instantaneous turning rate, ω_{max}, whereas the mean of all values during a trial was the average turning rate, ω_{avg}.

Results

A total of 50 turns performed by six turtles were analyzed. Turtles remained level (i.e. did not bank) throughout the turns. All turns were continuously powered by movements of the fore- and hindlimbs. Two types of turns were identified: forward-moving predatory turns (*N*=43) from five individuals, and non-predatory backward turns (*N*=7) from one individual. Each type of turn was characterized by distinct patterns of limb movements and different levels of performance.

Limb kinematics

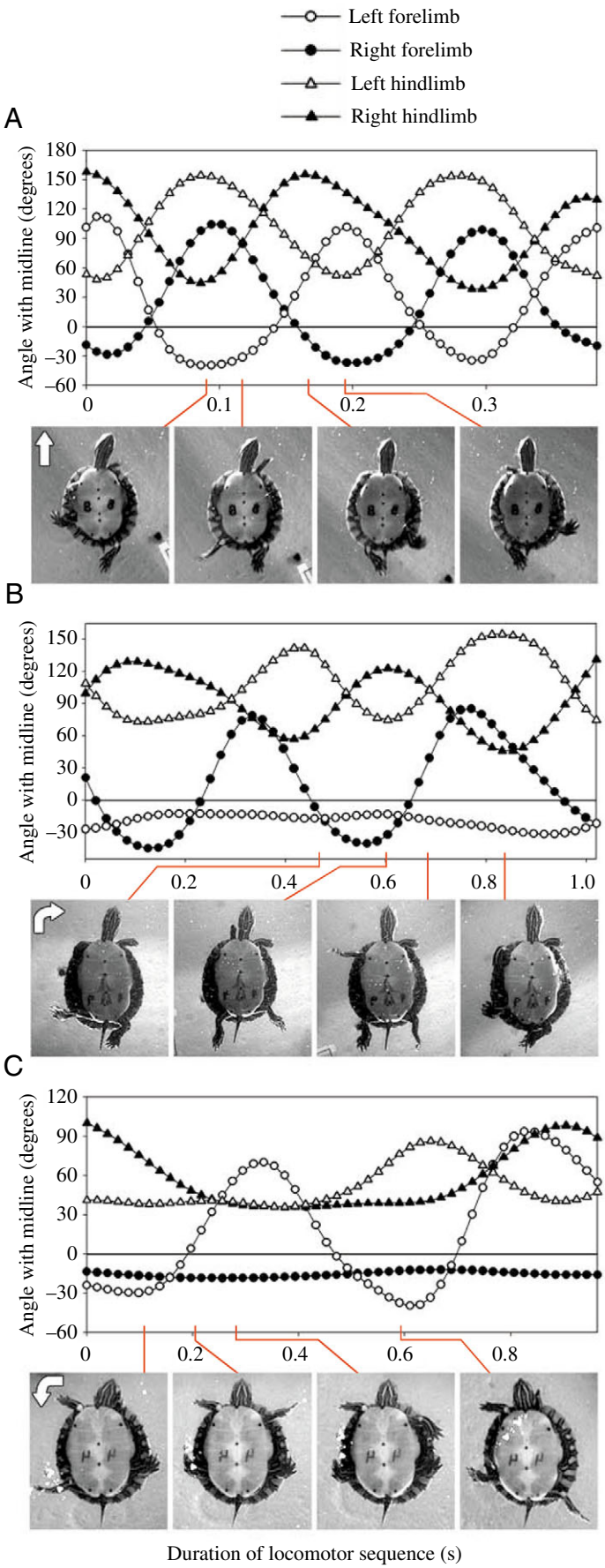
Forward and backward turns showed distinct kinematic patterns. In order to describe the movement of limbs during forward swimming we will follow the terminology used by Fish and Nicastro (Fish and Nicastro, 2003) and use ‘inboard’ to describe the side of the turtle facing toward the center of the turn, and ‘outboard’ to refer to the side facing away from the center of the turn. In forward turns, turtles maintain velocity while executing turns by alternating movements of the hindlimbs, similar to the pattern of hindlimb movement employed during rectilinear swimming (Fig. 2A,B). However, during rectilinear swimming, synchronous movements of contralateral fore- and hindlimbs appear to help maintain a straight trajectory. In forward turns the pattern of forelimb motions is modified. During forward turns, the inboard forearm is held in a protracted position throughout the turn (Fig. 2B); this should increase drag on the inboard side, allowing the forelimb to function as a pivot (Fish and Nicastro, 2003). The outboard forelimb continues to move as in rectilinear swimming, producing torque (i.e. a turning moment) about the inboard pivot and effecting the turn. The outboard forelimb moves in alternation with the ipsilateral hindlimb and synchronously with the contralateral hindlimb (i.e. maintains the pattern of movement seen in rectilinear swimming; Fig. 2B).

Limb movements for backward turns differ substantially from those for forward turns. From a forward trajectory or stationary position, a turtle can begin moving backward by synchronously protracting both hindlimbs. Once a turtle is moving backward, a turn can be initiated by additional limb movements. Although the pattern of limb movements used to produce backward turns is less stereotyped than that of forward turns, a general sequence of movements, in which turtles retract the forelimb on one side and protract the contralateral hindlimb (these two motions overlap temporally), is still apparent for most backward turns (Fig. 2C). This produces a torque about the center-of-rotation and initiates the turn. Following retraction of the forelimb, the ipsilateral hindlimb (which had been held in a relatively motionless protracted position) is retracted, providing additional thrust to the turn.

Turning performance

The smallest *R*/*L* was 0.0018 *L* (Table 1) and occurred during a forward turn with an average tangential velocity (U_{avg}) of $1.26\,L\,s^{-1}$ and an average turning rate (ω_{avg}) of 134.4 deg. s^{-1}. The second smallest *R*/*L* for a forward turn was 0.0083 *L* and had a U_{avg} of $1.40\,L\,s^{-1}$ and a ω_{avg} of 166.9 deg. s^{-1}. These two turns were performed by two different individuals. The smallest *R*/*L* for a backward turn was 0.0091 *L* with a U_{avg} of $0.86\,L\,s^{-1}$ and a ω_{avg} of 115.1 deg. s^{-1}. All seven backward turns had *R*/*L* less than 0.1 *L*. In contrast, only 13 of the 43 forward turns (30.2%; with each of the five turtles performing at least one) had *R*/*L* less than 0.1 *L*. The maximum ω_{avg} for all turns was 247.1 deg. s^{-1} and was attained during a forward turn of 79.1° with an *R*/*L* of 0.2846 *L*.

In addition to showing different kinematic patterns, forward



and backward turns also exhibited considerable differences in performance. Unless otherwise stated, results are reported as the mean ± s.e.m. Turn angles ranged from 76.2° to 243.6° (mean, 118.0±5.1°) for forward turns, and from 113.0° to 200.0° (mean, 162.0±12.4°) for backward turns. The average center-of-rotation (COR) for forward turns was positioned at 30.9±2.4% of the body length, whereas for backward turns it was 66.7±3.6%. There was a significant relationship between tangential velocity (U_{avg}) and the COR for both forward and backward turns. Least-squares regressions indicated that the COR moved farther anterior as speed increased for forward turns, whereas for backward turns the COR moved farther posterior as speed increased (r^2=0.295 and r^2=0.772, respectively; P<0.01). Forward turns showed a weak, but significant, relationship (r^2=0.420; P<0.001; Fig. 3) between the average tangential velocity through the turn (U_{avg}) and the length-specific minimum instantaneous radius of the turning path (R/L); this relationship for backward turns was even stronger (r^2=0.863; P<0.01; Fig. 3). However, no relationship was found between angular velocity (ω_{avg}) and R/L for forward (r^2=0.001; P=0.878) or backward (r^2=0.259; P=0.244) turns (Fig. 4).

To further compare performance differences between forward and backward turns, for each of the six primary performance variables we calculated the extreme 20% (N=9) values for forward turns (Table 1). These extreme values included the minimum nine values for R and R/L and the maximum nine values for U and ω [following published precedents (Webb, 1983; Gerstner, 1999; Fish and Nicastro, 2003; Fish et al., 2003; Maresh et al., 2004)]. These values of R and R/L for forward turns were much more similar to those

Fig. 2. Representative kinematic profiles for three modes of swimming performed by painted turtles, with still images from a high-speed video indicating the position of the limbs (humerus and femur) at specific times during the locomotor sequence. Circles, forelimbs; triangles, hindlimbs; open symbols, right side of the body; closed symbols, left side. A decrease in the angle with midline represents limb protraction and an increase in the angle represents limb retraction. Arrows in the first still image of each sequence indicate the direction of movement during the sequence. (A) Representative kinematic profile of a painted turtle during level rectilinear swimming. Note the synchronous movements of contralateral fore- and hindlimbs and the alternating movements of the ipsilateral fore- and hindlimbs. (B) Representative kinematic profile of a turtle during a forward turn. This 82° turn had an average linear velocity (U_{avg}) of 1.83 L s^{-1}, resulting in an R/L of 0.24. The turtle propels itself forward using alternating movements of the hindlimbs. The inboard forelimb (open circle) is held in a protracted position for the entire turn and acts as a pivot. The outboard forelimb (closed circle) moves approximately in phase with the contralateral hindlimb, as in rectilinear swimming. (C) Kinematic profile of a backward turn. This 113° turn had an average linear velocity (U_{avg}) of 0.86 L s^{-1}, resulting in an R/L of 0.0091. The turtle used synchronous protraction of the hindlimbs to begin moving backward (not plotted). While moving backward, the right forelimb was retracted while the left hindlimb was protracted. During this time the other set of contralateral limbs were held motionless, after which the outboard hindlimb retracted to accelerate the turn.

Table 1. *Turning performance data*

	R (m)	R/L (L)	U_{avg} (L s^{-1})	U_{max} (L s^{-1})	ω_{avg} (deg. s^{-1})	ω_{max} (deg. s^{-1})
Minimum						
Forward	0.0001	0.0018	1.26	1.89	46.2	147.7
Backward	0.0005	0.0091	0.70	1.21	81.8	135.3
Maximum						
Forward	0.0551	1.0442	4.51	6.18	247.1	501.8
Backward	0.0049	0.0950	1.59	2.44	162.1	291.6
Mean						
Forward	0.0114 (0.0017)	0.2477 (0.0365)	2.52 (0.15)	3.62 (0.19)	136.4 (6.4)	312.0 (13.5)
Backward	0.0017 (0.0006)	0.0340 (0.0116)	1.04 (0.11)	1.67 (0.15)	128.0 (9.8)	221.9 (20.7)
Forward (extreme 20%)	0.0018 (0.0004)	0.0423 (0.0088)	3.97 (0.10)	5.47 (0.16)	198.4 (8.8)	434.0 (14.1)

Values in parentheses are standard error of the mean.

R, minimum radius of the turning path; L, body length; R/L, length-specific minimum radius of the turning path; U_{avg}, average linear velocity of the turn; U_{max}, maximum instantaneous linear velocity of the turn; ω_{avg}, average angular velocity of the turn; ω_{max}, maximum instantaneous angular velocity of the turn.

of backward turns; however, values of U and ω became substantially greater for forward turns than backward turns in this comparison.

Discussion

Mechanisms of aquatic turning in turtles

Because freshwater turtles have a rigid body and non-propulsory tail, which is reduced in most species, only the fore- and hindlimbs can be used to produce aquatic thrust (Pace et al., 2001). One focus of this study was to determine how painted turtles use their limbs to execute turns. Turns require an asymmetry in forces between the inboard and outboard sides of the animal, which could be produced through any of several different patterns of limb movement. Using a simplified descriptive framework, each individual limb might show one of four basic patterns of movement during a turn: (1) continue to move as in rectilinear swimming, (2) exhibit movements modified from the pattern used during rectilinear swimming, (3) fold along the body to stop contributing to propulsion, but minimize additional drag, or (4) project out from the body to increase drag and act as a pivot. For example, either one or both inboard limbs might show pattern 3 (fold along the body) while the outboard limbs show pattern 1 or 2 (standard-rectilinear or modified rowing). Alternatively, either one or both inboard limbs might show pattern 4 (outward projection as a pivot) while the outboard limbs show patterns 1 or 2 (standard-rectilinear or modified rectilinear rowing; powered turns) or 3 (fold along the body; unpowered turns). Our data show that, during forward turns, painted turtles consistently combine patterns 4 and 1, protracting the inboard forelimb and holding it stationary into the flow, while continuing to move the outboard forelimb and both hindlimbs as in rectilinear swimming. This combination of limb movements during forward turns is a fairly basic modification of the limb movements used for rectilinear swimming, which may simplify their neural control (Macpherson, 1991; Earhart and Stein, 2000). Moreover, the functional consequence of this movement

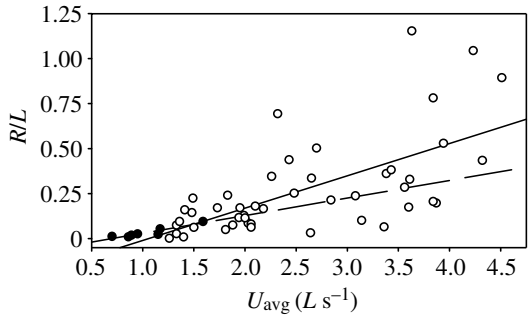


Fig. 3. Relationship between average tangential velocity (U_{avg}) and length-specific minimum radius (R/L) for forward and backward turns. Open symbols represent forward turns (N=43, solid regression line); closed symbols represent backward turns (N=7, broken regression line). Both relationships are significant (see text for regression statistics).

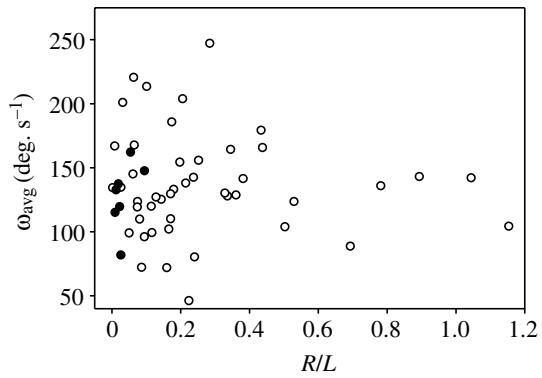


Fig. 4. Relationship between the length-specific minimum radius of the turning path (R/L) and average angular velocity (ω_{avg}). Open symbols represent forward turns (N=43); closed symbols represent backward turns (N=7). Neither relationship is significant (see text).

pattern is that swimming freshwater turtles execute forward turns by increasing inboard drag while still producing thrust, a combination of limb movements that should allow them to execute turns more quickly than alternative patterns (e.g. if any of the limbs were folded against the body). These patterns of turning kinematics are similar to those of another rigid-bodied species, the whirligig beetle (Fish and Nicastro, 2003), in which inboard limbs appear to function as a pivot about which the body rotates due to both initial forward momentum and forward thrust generated by the outboard limbs. In addition, because the left and right hindlimbs of turtles show similar patterns of motion during forward turns, it is the movements of the forelimbs in particular that appear to be responsible for generating the asymmetric forces required for turtles to execute turns. These findings support the conclusion of Pace et al. (Pace et al., 2001) that swimming freshwater turtles (except *Carettochelys* and possibly trionychid softshells) use their forelimbs primarily for balance and controlling orientation. Evaluations of the forces produced by each limb during turns [e.g. using techniques such as particle image velocimetry (Drucker and Lauder, 1999; Blob et al., 2003)] could further test this hypothesis.

In addition to forward turns, we also observed backward turns by painted turtles. Although generalizations about the performance of backward turns must be made with caution because all of our observations were from a single individual, we have also observed this type of turn in two other species of freshwater turtle (the slider, *Trachemys scripta*, and the softshell, *Apalone spinifera*; G.R. and R.W.B., unpublished), suggesting that it is not unusual for turtles to perform this behavior. The limb movements of backward turns are more complex than those of forward turns, but several distinctive characteristics can still be recognized. First, all backward turns occurred after the turtle, moving forward, approached the side of the arena and then reversed direction without rotating the body. Reversal was accomplished by synchronous forward sweeps of both hindlimbs with the hindfoot webbing fully extended. Davenport et al. (Davenport et al., 1984) observed that sliders (Emydidae) often swept both hindlimbs forward in unison to achieve rapid braking, so it is likely that the initial protraction of the hindlimbs during backward turns by painted turtles functions to stop forward momentum (rather than contribute to the turn) and that subsequent synchronous protractions generate the forward thrust used to reverse direction. Once turtles were moving backward, turns were initiated by near simultaneous retraction of one forelimb and protraction of the contralateral hindlimb, producing a turning moment that rotated the body.

In addition to differences in kinematics, several parameters of turning performance also differed between forward and backward turns (Table 1). For both forward and backward turns the COR moved closer to the leading edge of the body with increasing velocity. This resulted in a cranially positioned COR for forward turns and a caudally positioned COR for backward turns. Backward swimming was slower than forward swimming and also resulted in much lower angular velocities. In addition, the *R*/*L* for backward turns generally were much smaller than those for forward turns. However, when only the minimum 20% of values for forward turns are compared to values for backward turns these differences are minimized. In fact the two smallest turning radii were from forward turns. Still, the performance of backward turns was much less variable than that of forward turns, with the range of *R*/*L* spanning only one order of magnitude (0.0091–0.0950 *L*), whereas for forward turns *R*/*L* spanned four orders of magnitude (0.0018–1.0442 *L*). Similar comparisons of forward and backward turning performance in other aquatic taxa are available for only one other species, the angelfish [*Pterophyllum scalare* (Webb and Fairchild, 2001)]. In contrast to turtles, angelfish showed significantly larger length-specific turning radii (*R*/*L*) during backward turning (0.71) than during forward turning (0.41), a result that may relate to the differing positions of propulsive appendages in these species.

Comparisons with other taxa

Another focus of this study was to compare the turning performance of turtles with that of other taxa, particularly those with rigid bodies. Rigid-bodied animals that have been

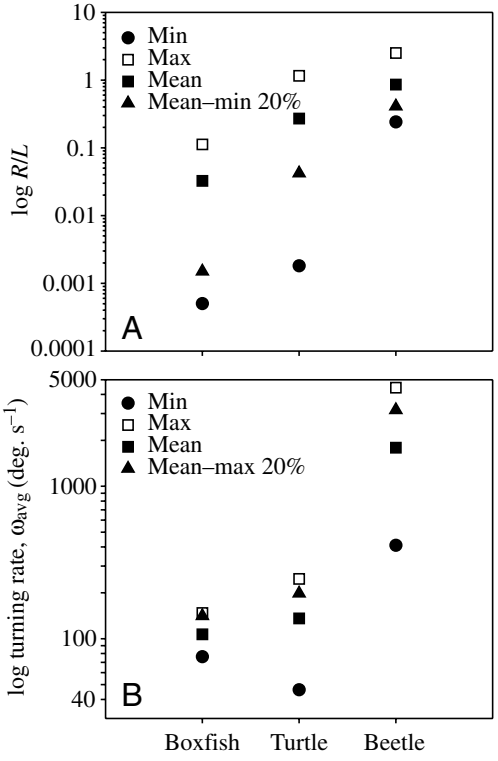


Fig. 5. Comparison of turning performance for three rigid-bodied taxa. (A) Length-specific minimum radius of the turning path (*R*/*L*). (B) Average turning rate (ω_{avg}). Closed circles indicate the single minimum value, open squares indicate the single maximum value, closed squares indicate the mean of all values, and closed triangles indicate the mean of the minimum 20% of values (A) or maximum 20% of values (B). Values for boxfish (*N*=12) are from Walker (Walker, 2000); values for beetles (*N*=119) are from Fish and Nicastro (Fish and Nicastro, 2003); values for turtles are from this study and include only forward turns (*N*=43). Data are graphed on a $\log_{10}$ scale.

examined to date have excelled in one of the two parameters of turning performance (agility or maneuverability), but not both. For example, boxfish are highly maneuverable (small *R*/*L*), but have low agility (Walker, 2000); in contrast, whirligig beetles can rotate with high agility (high angular velocities), but are not very maneuverable [i.e. they have large *R*/*L* (Fish and Nicastro, 2003)]. Our analysis of turning performance in painted turtles shows that when compared to other rigid-bodied taxa, rather than excelling at one of the two performance parameters, painted turtles display intermediate values for both (Fig. 5). For each of the four measurements of *R*/*L*, the same pattern of performance was identified for the three species: boxfish<turtle<beetle. Although the values for the painted turtles overlapped with both those of boxfish and the whirligig beetle, the maximum *R*/*L* of boxfish (0.1121 *L*) was smaller than the minimum *R*/*L* for the beetle (0.24 *L*). The pattern is the same for ω_{avg}, with boxfish<turtle<beetle, for all but the minimum values.

If comparisons are expanded beyond rigid-bodied taxa, differences in maneuverability between painted turtles and other taxa vary considerably depending on the criteria used. Table 2 shows *R*/*L* (maneuverability) values from 18 studies that have measured turning performance in a wide range of aquatic animals. These values are most often published as an average of all trials for a given species. However, other values are also frequently reported, either as a complement to overall means or in place of them, such as the average of the minimum 20% *R*/*L* values, or single, overall minimum values (e.g. Webb, 1976; Webb, 1983; Fish, 2002; Fish et al., 2003). The most conservative comparisons rely on the average of all trials. In this case, painted turtles have an average *R*/*L* (0.25 *L*) that is smaller than only four previously studied taxa: whirligig

Table 2. *Comparison of length-specific turning radii among taxa*

Species	Common name	Mean	Mean–min 20%	Min	References
Ostracion meleagris	Spotted boxfish	0.0325	0.0015	0.0005	(Walker, 2000)
Acanthurus bahanius	Ocean surgeonfish	–	<0.01	–	(Gerstner, 1999)
Thalassoma bifasciatum	Bluehead wrasse	–	0.02	–	(Gerstner, 1999)
Stegastes leucostictus	Beaugregory damselfish	–	0.04	–	(Gerstner, 1999)
Chrysemys picta	Painted turtle	0.25	0.0423	0.0018	This paper
Xenomystus nigri	Knifefish	0.055†	–	–	(Domenici and Blake, 1997)
Chaetodon capistratus	Foureye butterflyfish	–	0.06	–	(Gerstner, 1999)
Pterophyllum eimekei	Angelfish	0.065	–	–	(Domenici and Blake, 1991)
Squalus acanthias	Spiny dogfish	0.067	–	0.041	(Domenici et al., 2004)
Esox lucius	Pike	0.09†	–	–	(Domenici and Blake, 1997)
Zalophus californianus	Sea lion, male	–	0.11	0.09	(Fish et al., 2003)
Micropterus dolomieu	Bass	–	0.11	–	(Webb, 1983)
Coryphaena hippurus	Dolphin	0.13	–	–	(Webb and Keyes, 1981)
Pseudorca crassidens	False killer whale	–	0.15	0.13	(Fish, 2002)
Cephalorhynchus commersonii	Commerson's dolphin	–	0.16	0.15	(Fish, 2002)
Inia geoffrensis	Amazon River dolphin	–	0.16	0.10	(Fish, 2002)
Salmo gairdneri	Trout	–	0.17	–	(Webb, 1976)
Delphinapterus leucas	Beluga whale	–	0.17	0.15	(Fish, 2002)
Sphyrna lewini	Scalloped hammerhead shark	0.183	–	–	(Kajiura et al., 2003)
Salmo gairdneri	Trout	–	0.18	–	(Webb, 1983)
Orcinus orca	Killer whale	–	0.18	0.11	(Fish, 2002)
Zalophus californianus	Sea lion, female	–	0.19	0.16	(Fish et al., 2003)
Carcharhinus plumbeus	Sandbar shark	0.193	–	–	(Kajiura et al., 2003)
Tursiops truncatus	Bottlenose dolphin	–	0.19	0.13	(Fish, 2002)
Tursiops truncatus	Bottlenose dolphin	0.21	0.09	0.08	(Maresh et al., 2004)
Metynnis hypsauchen	Silver dollar	0.22	–	–	(Webb and Fairchild, 2001)
Seriola dorsalis	Yellowtail	0.23	–	–	(Webb and Keyes, 1981)
Lagenorhynchus obliquidens	Pacific white-sided dolphin	–	0.23	0.20	(Fish, 2002)
Spheniscus humboldti	Humboldt penguin	–	0.24‡	–	(Hui, 1985)
Carassius auratus	Goldfish	0.25	–	–	(Webb and Fairchild, 2001)
Pterophyllum scalare	Angelfish	0.41	–	–	(Webb and Fairchild, 2001)
Dineutes horni	Whirligig beetle	0.86	0.41	0.24	(Fish and Nicastro, 2003)
Thunnus albacares	Yellowfin tuna	0.47	–	0.20	(Blake et al., 1995)
Illex illecebrosus	Short-finned squid	–	–	~0.5	(Foyle and O'Dor, 1988)

Species are ranked in order of increasing mean turning radius (*R*/*L*), using mean–min 20% in place of overall mean when available.
†When no information is given, values were considered to be overall means.
‡Data represent the minimum five *R*/*L* out of 39 trials (minimum 13%).

beetles [0.86 *L* (Fish and Nicastro, 2003)], squid [~0.5 *L* (Foyle and O'Dor, 1988)], tuna [0.47 *L* (Blake et al., 1995)] and angelfish [0.41 *L* (Webb and Fairchild, 2001)]. However, because the goal of our study was to examine maximal turning performance in turtles (in the context of predator–prey encounters), comparisons of minimum *R*/*L* values are also justified. In these comparisons, the mean-minimum 20% *R*/*L* for painted turtles (0.0423 *L*) was smaller than the reported values for all but four previously examined species: damselfish (0.04 *L*), wrasse (0.02 *L*), surgeonfish (<0.01 *L*) and boxfish (0.0015 *L*) (Gerstner, 1999; Walker, 2000). Moreover, when single minimum *R*/*L* values are compared, only the boxfish (0.0005 *L*) and possibly surgeonfish (<0.01 *L*; reported as mean-min 20%) have turning radii smaller than painted turtles (0.0018 *L*). As seen with boxfish, these comparisons indicate that the rigid bodies of painted turtles do not appear to severely limit their maneuverability.

Agility (ω) also varies considerably among taxa (Fig. 6). The maximum ω_{avg} for turtles (247 deg. s^{-1}) is greater than the values for boxfish [147 deg. s^{-1} (Walker, 2000)] and squid [90 deg. s^{-1} (Foyle and O'Dor, 1988)], but less than those for beetles [4438 deg. s^{-1} (Fish and Nicastro, 2003)], stiff-bodied tuna [426 deg. s^{-1} (Blake et al., 1995)] and penguins [576 deg. s^{-1} (Hui, 1985)]. In addition, because body size appears to be an important underlying determinant of agility (Fish and Nicastro, 2003), the fact that much larger stiff-bodied cetaceans can turn at comparable rates suggests that they are much more agile than rigid turtles. Similarly, the fact that flexible fish of similar size are able to turn at rates much higher than turtles (Fig. 6) suggests that agility may be constrained by a rigid design.

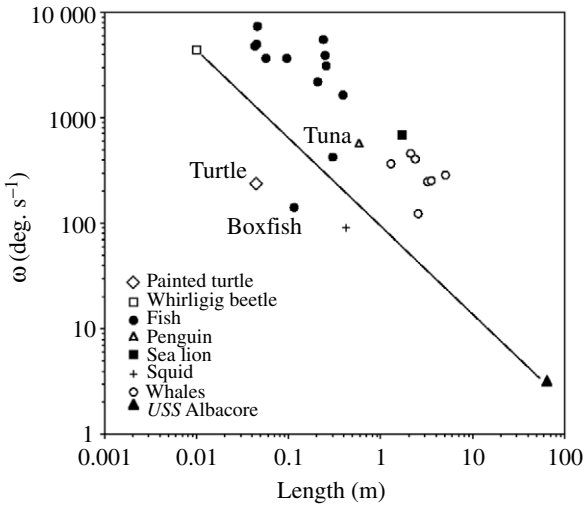


Fig. 6. Comparison of turning rate, ω_{avg}, with respect to size among a broad range of taxa graphed on a $\log_{10}$ scale. The line connects the beetle and submarine (*USS* Albacore), both of which have rigid bodies. Other rigid-bodied taxa appear to the left of the line. Modified from Fish and Nicastro (Fish and Nicastro, 2003) with permission. Value of ω_{avg} for turtles based on this study; position of boxfish data point moved to reflect ω_{avg} rather than ω_{max}.

Modes of turning and performance

That two of the three smallest reported *R*/*L* values are from rigid-bodied taxa, boxfish (Walker, 2000) and turtles (this study), suggests that rigid-bodied taxa use modes of turning that increase maneuverability. In fact, having small turning radii may be of particular importance to rigid taxa because it is the only way to decrease the space required for them to complete a turn. In contrast, flexible taxa can reduce the area required to turn simply by bending their bodies (Walker, 2000). However, rigid-bodied whirligig beetles turn with relatively large radii (Fish and Nicastro, 2003). Reasons for these differences between low and high *R* among rigid-bodied taxa, as well as for the discrepancy in agility between flexible- and rigid-bodied taxa, may be based on the modes of turning used by these different groups.

Aquatic organisms can generate turning forces (i.e. torque) by two mechanistically different methods: (1) actively, by motion of control surfaces, or (2) passively, from flows produced by movements of the body or external flow fields (Fish, 2004). Passively powered turns rely on the kinetic energy of a translating body or extended hydrofoil moving through local flow, and therefore require that turning path (*R*) and tangential velocity (*U*) be greater than 0. The effectiveness of passively powered turns should vary with speed, with torque production increasing with the square of velocity (Weihs, 1981). As a result, at low *U*, passive maneuvering becomes more difficult (Weihs, 1981; Fish, 2002). In contrast, actively powered turns are generated by oscillating limbs, and although *R* and *U* may be greater than 0, this is not required. Oscillating limbs have a distinct advantage over passive maneuvering when *U*=0, as oscillating limbs produce hydrodynamically derived drag without movement of the body (Blake, 1986). This allows turns to be composed of pure rotational movements with no body translation (Walker, 2000). As a result, it seems that oscillating limbs are a better design for maneuverability (lower *R*). However, there are several reasons why actively powered turns should reduce agility compared to passively powered turns regardless of whether the turn involves body translation. The first is that an object turning in place (*R* and *U*=0) will have higher pressure drag resisting rotation because the angle of attack between the body and the local flow is close to 90° along the entire length of the body (Walker, 2000). As long as an organism is designed to reduce drag while moving in a longitudinal direction, the angle of attack between the body and the local flow (and thus drag) will be reduced as *R* increases, being lowest while moving in a straight line. This is particularly the case for rigid-bodied taxa that cannot bend their bodies in the direction of the turn (Walker, 2000). A second reason that actively powered turns might suffer reduced agility is that for turns with translation (*R* and *U*>0), the rate of rotation is dependent on the speed of the oscillating limbs, the latter of which is reduced overall as a result of having distinct power and recovery strokes. In addition, paddling is inefficient at high *U* because the speed differential between the body and the paddle becomes smaller with less propulsive force being generated (Blake, 1986; Fish, 1996). In contrast, passively

powered turns utilize much higher tangential speeds and have the advantage that turning forces can be generated without incurring a large decelerating drag.

These ideas help to explain the patterns of maneuverability and agility that are observed for the three rigid-bodied taxa examined to date. Turtles and boxfish are able to turn with a small R because their use of oscillating appendages does not depend on tangential velocity. In addition, although velocity is generated by oscillating limbs in whirligig beetles, their high angular velocity is achieved by having very high tangential velocity (U) while traveling along a large R. Lastly, flexible-bodied organisms can have high levels of maneuverability and agility, but they also have the ability to mix styles of turning, whereas most rigid-bodied taxa appear to be limited to actively powered turns using oscillating limbs.

Morphological correlates of turning performance

Differences in agility between painted turtles and boxfish may not relate exclusively to their differences in body size (Fig. 6). Walker (Walker, 2000) gives three reasons why the rigid bodies of boxfish should limit agility: (1) an inability to bend the cranial end of the body into the turn, (2) an inability to bend and reduce the body's second moment of area about the rotational axis, resulting in high inertial resistance to rotation (Carrier et al., 2001; Walter and Carrier, 2002), and (3) high pressure drag resisting rotation because the angle of attack between the body and the local flow is close to 90° along the entire length of the body. Because turtles are also unable to bend their bodies, they must also face the same constraints on agility posed in points 1 and 2. However, painted turtles are more dorsoventrally flattened and have more rounded dorsal profiles than boxfish, both of which should reduce the pressure drag to which turtles are exposed.

Despite having rigid bodies, painted turtles may also be able to reduce second moments of area through mechanisms unavailable to boxfish. First, with very few exceptions (e.g. snapping turtles), most extant turtles have highly reduced tails (Willey and Blob, 2004). The presence of a long tail in swimming turtles would increase both the second moment of area and rotational inertia, which would result in decreased agility (Carrier et al., 2001). Therefore, tail reduction in turtles may be a factor contributing to their greater agility in comparison to boxfish. In this context, it is perhaps not surprising that those turtles that possess long tails (chelydrines) are primarily benthic scavengers or ambush predators that do not actively pursue evasive prey, for which high turning performance might be required (Ernst et al., 1994).

Other morphological features of turtles that may help enhance their agility compared to boxfish relate to the propulsors, or control surfaces. The fins of boxfish are supported by flexible rays, whereas the limbs of turtles are supported by more robust, stiffer limb bones that can extend farther from the body than boxfish fins. These differences in structure may help make turtle limbs a more effective brake or pivot on the inboard side, and a more powerful propulsor on the outboard side. In addition, the position of the limbs in turtles, with all four located near and approximately equidistant from the center of rotation, might also enhance maneuverability (Fish, 2002). Furthermore, because all four limbs in turtles lie within the same horizontal plane, thrust and drag forces used to generate torque are all directed within the plane of rotation. Boxfish also achieve enhanced maneuverability by using multiple control devices [i.e. five fins (Gordon et al., 2000; Walker, 2000; Hove et al., 2001)], but multiple fins located outside a single plane of rotation may be less effective contributors to horizontal (i.e. yawing) turns.

Directions for further study

As noted by Walker (Walker, 2000), morphologies that might facilitate or limit turning have been widely discussed, but the effects of many design features on turning performance remain unresolved. Numerous studies have examined the effect of body and fin shape on turning performance among fishes and have identified morphological features correlated with turning performance (Gerstner, 1999; Schrank and Webb, 1998; Schrank et al., 1999). Similarly, it is possible that interspecific variation in the morphology of turtles could also produce substantial differences in turning performance. Although the general body plan of turtles has changed little over 200 million years (Gaffney, 1990; Rieppel and Reisz, 1999), extant freshwater turtles exhibit considerable morphological diversity. For example, softshell turtles of the genus *Apalone* are dorsoventrally flattened to an even greater degree than the painted turtles examined in this study, and possess extensive webbing on the forefeet (Webb, 1962; Pace et al., 2001). As a result, these highly aquatic species might be expected to exhibit turning performance superior to that of painted turtles. In contrast, many species of the riverine genus *Graptemys* (map turtles) have prominent mid-dorsal keels (Ernst et al., 1994). It is possible that, like the keels of boxfish (Bartol et al., 2003; Bartol et al., 2005), the keels of map turtles may aid in stabilization during rectilinear swimming, which in turn could negatively affect turning performance. Correlating parameters of turning performance (maneuverability and agility) with predator–prey interactions and habitat characteristics (e.g. flow velocity and turbulence) could help to determine the factors that have influenced the diverse morphologies seen within turtles as well as the broad impact of rigid body designs.

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